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Influence of external factors in the survival and reproductive success of the Loggerhead turtle, *Caretta caretta*, in Maio Island, Cape Verde

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Resumo

As tartarugas marinhas são criaturas peculiares, com ciclos de vida complexos e dinâmicos, capazes de realizar longos trajetos migratórios entre vários tipos de habitats. Graças às características da sua história de vida - desde a sua fenologia e distribuição às suas características fisiológicas (organismos ectotérmicos) e anatómicas - as tartarugas marinhas são altamente vulneráveis a inúmeras ameaças que afetam diretamente a sua sobrevivência, ou que indiretamente limitam o seu sucesso reprodutivo. Embora todos os estágios de vida estejam suscetíveis a ameaças, a maioria da informação acerca das mesmas está concentrada nos primeiros estágios, ocorrem em meio terrestre, uma vez que é mais acessível obtê-la. Durante o processo de incubação em praias arenosas, os embriões estão dependentes das condições ambientais da areia envolvente que por sua vez influenciam fatores como o teor em humidade, concentração de gases e temperatura, responsáveis por um correto desenvolvimento.

O equilíbrio hídrico entre o embrião e o meio é fundamental para, por um lado, evitar perdas de água por evaporação, causando dessecação e, por outro lado, para evitar a morte por asfixia ao condicionar as trocas gasosas. Dependendo da localização do ninho na praia e das características topográficas da mesma (largura, elevação em relação ao mar, etc.), os ninhos estão mais ou menos propensos a eventos de inundação. Eventos momentâneos e esporádicos podem beneficiar o processo de incubação ao renovar o conteúdo de água bem como ao reduzir a temperatura do meio envolvente. Contudo, eventos de maior duração e com maior ocorrência, que ocorrem frequentemente em ninhos colocados junto ao nível da maré alta e em praias com maior propensão para inundação, podem levar à inviabilização total da ninhada.

A temperatura, para além de ser responsável por inúmeros processos biológicos e fisiológicos destes seres ectotérmicos enquanto adultos (p.ex. distribuição, fenologia, hábitos alimentares e taxas de crescimento), está altamente associada aos processos reprodutivos. O Intervalo de Tolerância Térmica (ITT) define a gama de temperaturas em que os embriões podem desenvolver-se corretamente, sendo que temperaturas acima ou abaixo desses limites térmicos por períodos estendidos podem causar stress ou mesmo morte embrionária. A determinação sexual das crias é igualmente reflexo da temperatura ambiente, com temperaturas mais altas a gerar mais fêmeas, e temperaturas mais baixas a produzir mais machos.

Considerando o panorama das alterações climáticas, o aumento previsto da temperatura ambiente representa uma potencial ameaça à sobrevivência e ao sucesso reprodutivo das tartarugas marinhas. Subidas ligeiras de temperatura podem representar alterações severas na dinâmica da população ao condicionarem a etapa reprodutiva. Por exemplo, em muitas populações de Tartarugas-comum de todo o mundo, já se regista um grande desvio no rácio dos sexos das ninhadas para o sexo feminino. A contínua subida de temperatura pode levar à total feminização das ninhadas, o que no futuro poderá levar a problemas de infertilidade. Ainda, caso a temperatura da areia atinga valores acima do limite térmico máximo suportado pelos embriões, o desenvolvimento embrionário pode ser comprometido, levando à perda de coortes.

Para além das condições ambientais, fatores bióticos podem igualmente representar um perigo para a sobrevivência das ninhadas. A predação é uma das causas de mortalidade mais comum, mas também infeções fúngicas ou bacterianas são apontadas como frequente causa de morte em diversas praias de todo o mundo. Os mamíferos são os predadores mais reportados, contribuindo para grandes níveis de mortalidade de ninhos de tartarugas, mas também pássaros, répteis e crustáceos têm-se revelado grandes predadores de tartaruga marinha em algumas praias.

O arquipélago de Cabo Verde, na costa Oeste de África, abriga a terceira maior subpopulação de Tartaruga-comum (*Caretta caretta*) do mundo. O caranguejo-fantasma *Ocypode cursor* é atualmente o maior predador de ninhos nas praias de Cabo Verde. Este organismo semi-terrestre é altamente dependente do teor em humidade para respirar pelo que apresenta um comportamento notívago e crepuscular. Os indivíduos mais novos têm uma dispersão mais reduzida, limitando-se essencialmente

à zona da linha da maré, contudo, os indivíduos maiores são capazes de cobrir grandes extensões das praias, incluindo as zonas de desova das tartarugas. O seu impacto predatório tem sido amplamente estudado em praias da Ilha da Boavista, onde mais de 50% dos ninhos podem ser afetados, mas pouco se sabe sobre a sua ação nas praias das restantes ilhas.

O objetivo principal desde estudo passa pela melhor compreensão do impacto das diversas fontes de mortalidade no sucesso reprodutivo de Tartaruga-comum (*Caretta caretta*) do mundo, mais propriamente o impacto 1) da predação por caranguejos-fantasma, 2) da inundação e 3) da temperatura.

A grande heterogeneidade de coloração nas praias na Ilha do Maio permitiu conduzir um estudo pioneiro em Cabo Verde, e provavelmente no mundo, ao conjugar o impacto de vários fatores ambientais na mesma linha temporal. Isto é, considerando que diferentes colorações de areia implicam diferentes gamas de temperatura, foi possível avaliar em simultâneo o impacto direto da predação por caranguejos-fantasma, da inundação e da temperatura da areia no sucesso dos ninhos de Tartaruga-comum, bem como a possível relação entre esses fatores.

Dessa forma, foram monitorizados diariamente 70 ninhos de modo a avaliar o impacto direto da predação e da inundação na incubação, bem como o impacto de outras causas (p.ex. temperatura) por método indireto, como reflexo da mortalidade derivada de causas que não a predação nem a inundação.

O impacto da predação e o impacto de outras causas, como a temperatura, mostraram-se relacionados com a coloração da areia, contrariamente ao impacto da inundação, que se mostrou mais relacionado com outras características da praia, como a hidrodinâmica (limites das marés, energia de ondas) e a topografia das praias (largura, elevação, inclinação). Os ninhos do viveiro revelaram o maior sucesso de eclosão (≈76%) e consequentemente menor taxa de mortalidade, significativamente diferentes dos ninhos do meio natural, o que reforça o impacto positivo da implementação desta técnica.

Tal como esperado, as praias mais escuras revelaram ser as praias menos adequadas à incubação de ninhos de Tartarugas-comuns, com uma média de mortalidade de quase 80%, contrariamente às praias brancas cujo impacto da mortalidade foi aproximadamente 54%.

Os resultados das praias escuras não só se destacaram por revelarem a maior taxa de mortalidade, mas também porque, contrariamente ao esperado, revelaram a maior densidade de caranguejos-fantasma e a maior taxa de predação de ninhos, sugerindo que as elevadas condições térmicas, encontradas nessas praias, não parecem afetar a sobrevivência destes predadores.

As praias mistas, embora com coloração intermédia, sobressaíram pelos seus resultados opostos aos das praias escuras: menor densidade de caranguejos-fantasma e, consequentemente, menor taxa de predação. Isto sugere a existência de um fator extrínseco à temperatura, que condiciona a sua sobrevivência e atividade predatória, o que justifica os resultados obtidos. Estas praias destacaram-se ainda pela elevada taxa de mortalidade devido a outras causas como a temperatura.

As praias claras revelaram-se as mais adequadas para a incubação de ninhos de Tartaruga-comum pois, apesar do impacto de causas como a temperatura ter sido semelhante entre praias escuras e claras (≈25%), a disparidade de valores de mortalidade total entre as mesmas deveu-se essencialmente ao elevado impacto da predação nas praias escuras.

A coloração da areia foi um fator importante no sucesso reprodutivo das tartarugas não só pela temperatura associada, mas também pela sua influência na ecologia de um dos maiores predadores de ninhos, o caranguejo-fantasma. Estes caranguejos não parecerem ser afetados diretamente pelas condições térmicas das praias. Outro fator extrínseco à temperatura, e essencialmente associado às praias mistas, parece limitar a densidade dos mesmos, bem como o seu impacto predatório sobre os ninhos. Futuros trabalhos de investigação permitirão responder às questões levantadas por este estudo e com certeza tomar decisões conservativas mais acertadas, que proporcionem um melhor futuro a esta e a outras subpopulações de Tartarugas-comum.

Palavras-chave: coloração da areia, sucesso reprodutivo, *Caretta caretta*, *Ocypode cursor*, impacto térmico

Abstract

The main purpose of this project was to better understand the impact of the various sources of mortality on the reproductive success of the third largest sub-population of the loggerhead sea turtle (*Caretta caretta*) in Cape Verde, more precisely the impact of predation by ghost crabs, inundation phenomena and temperature.

Although sporadic inundation events may benefit the incubation process by renewing the water content and reducing the temperature of the surrounding environment, more intense and frequent events can asphyxiate the embryos and lead to total clutch loss. Temperature also plays an important role on reproduction by controlling the embryonic development, defining the sex ratio of the clutch and predicting the offspring fitness. Extreme temperatures may lead to total feminization of the clutch or compromise the embryos viability. Biotic features, such as fungal infections and depredation can also represent great hazards to nest success. In Cape Verde beaches, the main nests predator is the ghost crab (*Ocypode cursor*), which can predate more than 50% of the nests.

The great heterogeneity of coloration on the beaches in the Island of Maio allowed to enrol in a pioneering study in Cape Verde, and probably in the world, combining the impact of several environmental factors on the same timeline. That is, considering that different sand colorations imply different temperature ranges, it was possible to simultaneously assess the direct impact of predation by ghost crabs, inundation and sand temperature on the success of loggerhead sea turtle nests, as well as the possible interaction between these factors.

The results showed an absence of interaction between sand coloration and inundation impact. On the other hand, predation and other mortality causes such as temperature, were clearly related to the color of the sand. As expected, the darker beaches proved to be the least suitable beaches to incubate loggerhead sea turtle nests, with almost 80% of mortality rate. Not only temperature contributed to eggs mortality, but also, and contrary to what was expected, the density of ghost crabs and, consequently the predation impact was significantly higher on those beaches. The mixed beaches stood out for its opposite results, by recording the lowest crabs' density and the lowest predation impact of all beach type, and the highest mean mortality rate by other causes as temperature. The light beaches revealed to be the most suitable type of beach for nesting, by showing the lowest mean mortality rate, with predation and other causes impact having similar influence.

Sand coloration proved to be an important factor in the reproductive success of turtles not only due to the associated temperature, but also because of its influence on the ecology of one of the greatest nest predators. Although they do not appear to be affected directly by thermal conditions, another temperature-extrinsic factor, and essentially associated to mixed beaches, seems to limit their density as well as their predatory impact on nests. Future research will allow to answer the questions raised by this study and certainly take decisions that provide a better future for this and other subpopulations of loggerhead sea turtles.

Keywords: sand coloration, reproductive success, *Caretta caretta*, *Ocypode cursor*, thermal impact

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Chapter 1

General Introduction

1. General features of Loggerhead sea turtle (*Caretta caretta*, Linnaeus, 1758)

Sea turtles are among the largest living reptiles and are found in tropical, sub-tropical and temperate habitats around the world. They are intriguing animals, known for having a complex life history, mainly due to the diversity of ecosystems they use during their life time, including terrestrial habitats, coastal waters and the open ocean (Bolten, 2003). They are the only reptile performing long-distance migrations due to their air-breathing features, hydrodynamic shape, large size and powerful front flippers. All seven extant species are at risk of extinction, and considered Critically Endangered, Endangered or Vulnerable, according to IUCN Red List (2015).

Loggerhead sea turtle, *Carreta caretta* (Lnnaeus, 1758) is the most studied and the most widespread sea turtle species in the world, living and nesting in subtropical and temperate regions of the Atlantic, Indian and Pacific Oceans and the Mediterranean Sea (Dodd, 1988; Wallace et al., 2010). This species has a large head (which gives it its name) and a reddish-brown carapace. Due to their strong jaws, they are primarily carnivores throughout their life, eating mainly hard-shelled preys (such as crabs and snails) but consume also small amounts of seaweed or sargassum (Witherington, 2002). Initially, post-hatchlings and early juveniles feed essentially on pelagic organisms, while neritic loggerheads (grown individuals) feed primarily on benthic organisms (pelagic to benthic prey shift).

Ten subpopulations of this species can be found around the world, with their own population features (e.g. size and trends), geographical habitats and threats**.** The most endangered subpopulations are the North East Indian (Casale, 2015a), North West Indian (Casale, 2015b) and South Pacific (Limpus and Casale, 2015) that are considered Critically Endangered; the second most endangered is the North East Atlantic subpopulation, with Endangered classification (Casale and Marco, 2015), where the Cape Verde archipelago is considered the main rookery, hosting more than 95% of loggerhead nesting on the entire eastern Atlantic (Marco et al., 2012, 2010).

Five of the seven extant turtle species can be found in Cape Verde waters (López-Jurado et al., 2000; Marco et al., 2011), with loggerhead sea turtle, *Caretta caretta*, being the most common sea turtle in Cape Verde. Currently, this is the only species using Cape Verde sandy beaches to nest every year, however, there have been some occasional sightings of green turtle (*Chelonia mydas*) nesting in Maio Island (personal observation) since 2016. Due to the massive amount of turtles nesting every year (8000-30000 nests per year; Martins et al., 2015), Cape Verde is considered the third largest loggerhead nesting population worldwide – lead first by the Florida and Oman populations – and the second most important in the Atlantic (Marco et al., 2011).

All islands appear to have nesting activities (López-Jurado et al., 2000), however, the nest density per island varies (Martins et al., 2015). Boa Vista Island seems to host the majority of nests in Cape Verde (around 70-80%, with inter-annual variations). Maio and Sal Islands hosts *ca*. 6 to 8% each and Santa Luzia has lower abundance with around 4% of all nests. Santo Antão, San Vincente, Fogo and Santiago have very few nests per year (≈ 1%, although this is not absolute since there are some islands and islets poorly sampled). Brava Island does not have sandy beaches so there are no nesting activities there, but one of its two islets (Ilhéu de Cima) records 300 to 1000 nests annually (Martins et al., 2015).

Monzón-Argüello et al. (2010) showed, through DNA studies, that the Cape Verde loggerhead turtle population is genetically distinct and, therefore, reproductive isolated, from other loggerhead populations in the Mediterranean and Atlantic, and despite the philopatry observed in this species, there is a great gene flow between islands ("great plasticity in nesting fidelity") (Abella et al., 2010). Due to these facts, the Cape Verde loggerhead population can be considered an independent management unit (Wallace et al., 2010) with several rookeries (Monzón-Argüello et al., 2010).

2. Life history

The inicial stages of the turtle life cycle, which include oviposition, embryonic development and hatching, occur in terrestrial environment, more specifically in sandy beaches, and they are similar among all species (Bolten, 2003). After hatching, the hatchlings crawl down the beach to the sea, where they start to swim vigorously and rapidly for days – called "swim frenzy stage" – until their yolk resevoir ends (Wyneken and Salmon, 1992).

After this point *(post-hatchling transitional stage; Bolten, 2003)* they start to feed and initiate one of the three basic developmental journeys sugestted by Bolten, 2003): (a) neritic complete development, which means that turtles whole life is passed in neritic zones, with the exception on the nesting season, which occurs inland; (b) oceanic complete development, that is, post-hatchlings, when entering the sea, swim directly to open ocean zones and stay there until reach the age of reproduction; (c) an intermediate life history pattern, in which early development (post-hatchlings and early juveniles) occurs in open ocean zones and the late juveniles occur in neritic zones. The loggerhead sea turtle, *Caretta caretta* (Linnaeus, 1758) is the best-known example of intermediate life history pattern (Bolten, 2003).

At first, the early stages, when post-hatchlings reach the sea (the so called "lost years"), were a mystery and little was known about the real distribution, feeding habits and threats afecting 5-cm sea turtles. In 1986, Carr (1987, 1986) hypothesided that post-hatchlings swim frantically to convergence zones where they can feed and grow. The hidrodynamic of these areas lead to downwelling forces that collect anything bouyant around. So, these areas are exceptional for collecting and maintaining nutrients and food, and may have an eventual shelter effect (Carr 1987). Posterior studies have confirmed Carr's hypothesis for loggerhead turtles (Bolten et al., 1998; Bowen, 1995).

The North West Atlantic subpopulation has the best-known life cycle. Studies demonstrated that some juveniles can enter in Gulf of Mexico Stream and stay in the Sargassum Sea, during their early development (Witherington, 2002; Witherington et al., 2012). Sargassum grounds, which are found near the North West coast of Atlantic are an excellent example of these converging areas, and it is known that loggerhead juveniles spend their time there acting like low-energy, opportunistic predators (Frick et al., 2009), before recruiting to their neritic feeding grounds. Other individuals may enter the North Atlantic Gyre and perform long-drifts to the Atlantic East coast, near Azores and Madeira or even enter the Mediterranean Sea , while others can take different routes around the North Atlantic Ocean (Bolten et al., 1998).

Monzón-Argüello et al. (2012) recently showed that post-hatchlings from Cape Verde beaches may enter the North Atlantic Gyre as a result of secondary currents and stochastic storms, drifting predominantly westward to Atlantic zones (Madeira, Azores and the Canary Islands) or maybe to western Mediterranean waters (Monzón-Argüello et al., 2010) and return to West African waters several years later.

After the oceanic developmental stage, some juveniles exhibit homing behavior reaching natal waters (Bowen et al., 2004) to forage while others remain in pelagic waters. Some populations appear to have distinct (and sometimes more than one) feeding grounds for adults and juveniles, while others exhibit shared foraging zones (Bolten, 2003; Luschi et al., 2003).

Also, some individuals apparently switch between neritic and oceanic zones while adults. In populations such as the ones from Cape Verde (Hawkes et al., 2006), Japan (Hatase et al., 2002) Oman (Rees et al., 2010)(Rees et al., 2010)(Rees et al., 2010)(Rees et al., 2010)(Rees et al., 2010) and Florida, USA (Reich et al., 2010) there is an apparent phenotypic dichotomy between adult females. It seems that, in these populations, smaller adult loggerhead females adopt an ocean foraging strategy while larger adult females stay in neritic waters to forage. In fact, Cape Verde apparently differs from other regions by holding the majority of adults in the oceanic zones of Gambia and Guinea Bissau (Hawkes et al., 2006), rather than the neritic zones from Mauritania and Sierra Leone (Eder et al., 2012). This pattern may be explained by the fact that these regions are highly nutritional, due to high primary production, compared with other oceanic regions. Eder et al. (2012) suggested that this size dichotomy between these two habitats in Cape Verde may be explained by the fact that some late juveniles may reach and settle opportunistically in suboptimal but profitable oceanic waters in Cape Verde before discovering highly nutritional neritic waters. So, differences in size may not mean a ontogenic shift (and age disparity), but a difference in growth rates, which may correspond to the Compensatory Growth theory suggested by some authors (Bjorndal et al., 2003).

3. Nest characteristics

Little is known on whether nest placement results from selection criteria or if it is random, however some studies suggested sea turtles follow environmental cues such as sand moisture, temperature, slope, elevation above the water level and vegetation (Hawkes et al., 2009; Hays et al., 1995; Hays and Speakman, 1993; Kamel and Mrosovsky, 2004; Miller, 1997; Miller et al., 2003; Wilson, 1998; Wood and Bjorndal, 2000), which will determine micro environmental conditions for embryonic development. Wood and Bjorndal (2000) suggested that maybe loggerhead sea turtles do not use environmental factors as individual cues, but use it as an integrated cue based on environmental thresholds or based on environmental associations and its differences along the beach (Mazaris et al., 2006; Pike, 2008). In any case, nest site selection is crucial for clutch success since there are no parental cares. The environmental conditions of the selected site are the main driving-source of successful embryogenesis (Ackerman, 1997).

During incubation, three main parameters and its interactions will be essential for the embryonic development: gas exchange, moisture and temperature (Ackerman, 1997, 1980; Maloney et al., 1990; Mrosovsky and Yntema, 1980).

The gas exchange between eggs and the surrounding environment is very important to maintain vital gas proportions within the eggs (Ackerman, 1980; Maloney et al., 1990), being highly reliant on moisture content of the nest chamber. Eggs naturally change their weight during incubation (-10 to +30% of its initial mass) due to water vapor diffusion and water potential, without affecting embryogenesis (Miller et al., 2003). However, to avoid great losses of water, which may result in desiccation, a certain level of surrounding moisture is required (Maloney et al., 1990; Mcgehee, 1990). On the other hand, excess water contents for long periods may prevent the correct gas exchange, leading to suffocation (Ackerman, 1980; Kraemer and Bell, 1980; Ragotzkie, 1959).

Sand particle features of the nest chamber play an important role on embryonic development, since it defines other sand characteristics such as drainage, permeability, ventilation, water and salt retention, which in turn conditions the moisture and the gas exchange between eggs and surrounding environment (Ackerman, 1997, 1980; Foley et al., 2006; Mortimer, 1990). A recent study on the impact of small grain size of clay and silt substrate on loggerhead incubation process showed high levels of desiccation and mortality on eggs highly covered with clay and silt (Marco et al., 2017).

Along with gas diffusion and moisture parameters, sand temperature is also a significant factor that influences the incubation process (Ackerman, 1997), sex determination (Yntema and Mrosovsky, 1982), emergence success (Miller et al., 2003; Moran et al., 1999) and hatchling fitness (Carthy et al., 2003; Fisher et al., 2014). Typically, ectothermic embryos properly develop over a Thermal Tolerance Range (TTR) where above the maximum limit and below the minimum limit, embryonic development is compromised (Ackerman, 1997; Yntema and Mrosovsky, 1980). For sea turtles, temperatures above 33 ºC or below 24 ºC for an extend period increase egg mortality (Matsuzawa et al., 2002; Mcgehee, 1979; Yntema and Mrosovsky, 1980). Furthermore, the incubation period is negatively correlated with temperature, with higher temperatures resulting in a shorter incubation period and vice versa (Abella et al., 2007b; Matsuzawa et al., 2002).

Sea turtles are Temperature-dependent Sex Determination (TSD) organisms, which means that embryos' sex is defined by the nest chamber temperature during embryonic development, more precisely during the middle third of incubation (thermosensitive period; Mrosovsky and Pieau, 1991; Yntema and Mrosovsky, 1982). In sea turtles TSD pattern, low temperatures produce more males and high temperatures produce more females.

The Transitional Range of Temperature (TRT), in which both sexes can be produced in a mixed proportion, is around 26-28 ºC to 30-32 ºC for loggerhead sea turtle (Hulin et al., 2009; Milton et al., 1997; Mrosovsky and Pieau, 1991). Above the TRT only female hatchlings will be found in the clutch, and below the minimum transitional limit, the clutch will be composed by 100% of males. The constant prevailing temperature in which both males and females are produced in equal proportions (1:1 sex ratio) is called Pivotal Temperature and is highly accepted to be around 29 ºC for loggerhead *Carreta carreta*, with intra-specific variations (Ackerman, 1997; Mrosovsky, 1988; Mrosovsky and Pieau, 1991; Yntema and Mrosovsky, 1982, 1979).

Nest sand temperature is influenced by some external factors such as (a) diel and seasonal fluctuations of air temperature and its exchange to the sand column; (b) climatic events, e.g. rain and storms; (c) depth of the eggs, since eggs buried deeper are less prone to thermal fluctuations than eggs near the surface; (d) sand color, with darker sand reaching greater temperature values than lighter sand; (e) beach vegetation and (f) metabolic heat (Godfrey et al., 1996; Hays et al., 2001; Janzen, 1994a; Kamel, 2013; Matsuzawa et al., 2002; Morreale et al., 1982; Mrosovsky, 1988; Mrosovsky et al., 1984).

The metabolic heat, as a result of oxygen uptake, is influenced by the number of developing eggs within a nest (Broderick et al., 2001; Kaska et al., 2006) and may increase the chamber temperature by approximately 1 – 2 ºC (Matsuzawa et al., 2002; Mcgehee, 1979; Mrosovsky and Yntema, 1980). As a result, a temperature gradient can be found, with higher temperature at the center (Ackerman, 1997; Booth and Astill, 2001).

Hatchlings emergence and performance appear to be two other ecological processes that are controlled by sand temperature. Hatchlings tend to emerge only during the night, when sand temperature is lower. In fact there seems to be a critical thermal threshold above which hatchlings stop digging toward the surface and wait until sand temperature decreases again (Adam et al., 2007; Glen et al., 2006; Miller et al., 2003; Moran et al., 1999). Furthermore, hatchlings performance (e.g. crawl speed, swim activity) is an important factor that may determine lifetime fitness; an optimal thermal range during incubation appears to be around 28,5 – 31 ºC, whereas upper and lower temperatures lead to sub-optimal locomotor performance (Fisher et al., 2014).

4. Threats to survival and to reproductive success

Due to their peculiar features sea turtles are subject to innumerous threats, both inland and at sea. All life stages face natural threats, such as predation (essentially inland), natural diseases (e.g. pathogenic infections), parasites and environmental beach characteristics (e.g. temperature, nest inundation and erosion, vegetation, storm surges). The most severe threats are mainly caused by human activities that may result in sea turtles' death, or can cause indirect complications such as diseases or disabilities that may reduce their survival by affecting their migratory patterns, feeding habits and their reproductive behavior. In Cape Verde, the most man-induced threatening activities to sea turtle population is incidental catch (bycatch), poaching and coastal development (Casale and Marco, 2015; IUCN, 2015).

4.1. Man-induced threats

Adults and immature sea turtles, while crossing the ocean, are highly susceptible to industrial and artisanal fisheries, resulting in incidental take (bycatch). Most fishing gears and fisheries seem to have an impact on sea turtles by preventing them from rising and consequently drowning (such as gillnets, dredges, trawls, purse seine) or by severely injuring and incapacitating them. Longline and purse seine are the most common fisheries in Cape Verde waters. National and international legislations regulated some fishing quotes and fisheries (e.g. trawl activities are forbidden) in the Cape Verde Exclusive Economic Zone and obligate foreign vessels to acquire legal licenses. Nevertheless, the effective supervision of these measures is very poor on this country (López-Jurado et al., 2003).

Intentional capture (harvesting) is frequent in some places around the world, including the Cape Verde islands (López-Jurado et al., 2000; Marco et al., 2012, 2010, 2008). Males are usually hunted duo to the perceived aphrodisiacal power of their genitals (a popular belief in some parts of the world), not only for the consumption of the local population but also for the delight of tourists (Merino et al., 2007).

Females are also threatened by human poachers in nesting beaches (Cabrera et al., 2000). A recent report showed an average hunting pressure around 460 females/yr in Cape Verde islands (Martins et al., 2015). In this archipelago, and in others countries, poaching is mainly associated with meat and egg consumption, however, non-consumable uses as crafting of decorative objects, leather accessories, egg and shells collection is also common (López-Jurado et al., 2000; Marco et al., 2010).

Beach front constructions, mainly associated with tourism, have several implications that may reduce the quality of current suitable nesting beaches (Taylor and Cozens, 2010). The increase of tourism leads to an increase of trampled nests by people and off-road vehicles; the artificial lighting associated with constructions leads to disorientated nesting females and hatchlings, exposing them to poaching, predation and heat stress (Silva et al., 2017; Witherington and Martin, 2003); sand removal and sand nourishment are responsible for the alteration of the sand natural qualities (e.g. nutrients, grain

size and composition, height of beach, sand albedo) which may affect several incubation processes (Milton et al., 1997; Peterson and Bishop, 2005; Witherington and Martin, 2003).

Marine pollution is receiving more attention in the last few years and became another main anthropogenic threat, since it seems to impact all life stages of sea turtles (from eggs to adulthood). Organic contaminants, untreated waste, petroleum products (oil spills) and toxic metals are some of the products that may directly affect sea turtles' health causing death, or can accumulate in tissues and lead to diseases reducing their health and/or their reproductive success. (Camacho et al., 2013, 2012; Keller et al., 2004). Eggs and hatchlings are particularly affected by Persistent Organic Pollutants, since these products can be maternally transferred (Guirlet et al., 2010; Stewart et al., 2011), affecting the mechanisms that control the embryonic development (De Andrés et al., 2016; Keller, 2013).

Marine debris or marine litter, is another main cause of injury and death of marine biota (Laist, 1997). Sea turtles are a heavily affected species from ingestion and entanglement of plastic straps, lost and abandoned fishing gears ("ghost" nets) or other floating debris (Derraik, 2002; Laist, 1997). The loggerhead sea turtle (*Caretta caretta*) seems to be particularly susceptible to marine debris, mostly because of their migratory patterns and their feeding and nesting habitats (Casale et al., 2016; Gramentz, 1988; Hoarau et al., 2014; Nicolau et al., 2016; Ryan et al., 2016).

4.2. Environmental Conditions

Environmental features of the nesting beach also affect the reproductive success of the females, by interfering with micro-environmental conditions within the nest chamber (moisture, temperature and gas diffusion, mentioned above). Hydrodynamic and topographic features such as beach width and slope, tide amplitude and waves energy set out the natural sand accretion-erosion cycles, which in turn define the habitat availability and the propensity to flooding. Thus, nests placed in narrow beaches with lower slope and higher sea agitation may experience higher egg mortality than nests placed in wider beaches (Ackerman, 1997; Mcgehee, 1990, 1979).

Climatic conditions (e.g. precipitations, storm surges) may enhance natural beach dynamic and amplify beach erosion and inundation. Intensive rain may result in nests flooding by increasing water table or create water flow lines (runoffs) through nests that completely wash them away into the sea (Kraemer and Bell, 1980; Ragotzkie, 1959). Although storm surges are episodic events and result in short-term consequences, it may represent a great source of beach erosion, since these events tend to temporarily increase waves energy and height and tides level as well as, increase temporary rainfall intensity and frequency (Zhang et al., 2004, 2001).

4.3. Biotic threats

Eggs within nests near vegetation may experience desiccation or plant root invasion (Wood and Bjorndal, 2000) or may be benefited by the shade effect (Kamel, 2013). In the last case, eggs near plants may experience lower temperature within the nest chamber, and are more likely to survive than those away from vegetation, in beaches where sand temperature is extremely high (Janzen, 1994a; Kamel, 2013). Also, hatchlings from nests further inland and close to vegetation may become disoriented and trapped, risking being predated or exposed to excessive heat (Godfrey and Barreto, 1995).

Some pathogenic infections have been reported to affect juvenile and adult sea turtles (such as Fibropapillomatosis virus) by reducing their survival. Eggs can also be affected by pathogenic microorganisms, leading to embryonic stress or death. Fungal infection of sea turtles eggs may represent

a great hazard to sea turtle eggs around the world (Peters et al., 1994; Phillott and Parmenter, 2001), including in Cape Verde beaches, with *Fusarium spp*. representing a great source of mortality on Boa Vista nests (Abella et al., 2008; Sarmiento-Ramírez et al., 2010).

A recent study by Sarmiento-Ramírez et al. (2014) showed that the temperature range for optimal growth for two species of *Fusarium* (*F. falciforme* and *F. feratoplasticum*) overlap with temperature range for sea turtles developing eggs. Also, it showed that environmental conditions may determine the development of the disease as suggested by Sarmiento-Ramirez et al. (2010): nests susceptible to tidal flooding or with contents of clay/silt present higher signs of infection and incidence of disease by *Fusarium spp*..

Predation is one of the greatest natural threats to both eggs and hatchlings and may lead to mortality levels of ≈ 90% in some beaches (Dodd, 1988). Carnivorous mammals (as raccoons or fare dogs) are considered the most relevant sea turtles nest predators in some places (Ratnaswamy and Warren, 1998), but also sea birds (e.g. seagulls and crows), reptiles (e.g. lizards) and crabs (e.g. ghost crabs) can also prey on eggs within the nest or on juvenile sea turtles crawling down the beach (Dodd, 1988).

In Cape Verde, ghost crabs (*Ocypode cursor*, Linnaeus, 1758) are considered the main natural predator of sea turtle hatchlings and eggs (Marco et al., 2015, 2012), maybe due to the absence of predators to control them (Marco et al., 2015). This species belongs to a very conspicuous group of crabs, living in tropical and subtropical sandy beaches worldwide (Lucrezi and Schlacher, 2014). *O. cursor* inhabits the African West coast, from the south coast of Mauritania to the north coast of Namibia, and the eastern Mediterranean sandy beaches. This crab is an air-breathing semi-terrestrial invertebrate, highly dependent on a high level of moisture in its gills (the ventral portion of the respiratory organ) to ensure the oxygen uptake (Lucrezi and Schlacher, 2014; Warburg and Shuchman, 1979). Also, they have great water loss due to the permeability of the exoskeleton and their beach surface activity (Greenaway, 1988). Thus, to maintain the moist environment and restore the water loss, ghost crabs constantly absorb water from the sediment and from the swash zone (Wolcott and Wolcott, 2001) and show a nocturnal and crepuscular activity, remaining inside deep holes during the day, in the intertidal zone (Schuchman and Warburg, 1978).

Despite that, *O. cursor* seem to exhibit a great dispersal range, being able to move along the entire beach during the night. In fact, several studies reveal differences on spatial distribution of juveniles and adults along the beach in Cape Verde (Rodrigues et al., 2016; Vieira, 2011) and in Mediterranean (Strachan et al., 1999; Tureli et al., 2009). Smaller crabs seem to be concentrated near the water line while the large ones are mostly found near the shoreward limit of the crab zone. Also, a positive correlation between burrow depth and the distance from the water line (Tureli et al., 2009; Turra et al., 2005) suggest a greater capacity to dig deeper burrows by adults that allow them to accompany the depth of water table in drier areas. Schuchman and Warburg (1978), suggested that this spatial distribution of the individuals may be controlled by a sand moisture gradient, with smaller crabs having higher rates of water loss than the larger ones.

The trophic segregation according to body size suggested by Barton and Roth (2008) may be explained by this size dichotomy along the sea-to-shore axis. Larger crabs, who can explore drier areas (including nesting areas) feed at higher trophic level and therefore may be greater sea turtle consumers than the small ones, who cannot leave the water line zone. Also, Frederico (2013) showed that crabs

smaller than 20 mm cannot predate on sea turtle eggs and hatchlings, maybe due to their small claws and the absence of tufted eyes.

This kind of crab shows a great trophic plasticity by feeding on a large range of diet items: from small organic matter particles and macroscopic plant detritus (e.g. seagrass, seeds) to scavenging on dead animals (Strachan et al., 1999) and actively preying on small living vertebrates and invertebrates (apex invertebrate predator; Dodd, 1988).

It is known that ghost crabs have developed organs that allow acute senses of sight, smell, and hearing (Lucrezi and Schlacher, 2014 and citations). Frederico (2013) tried to understand what cues are used by *O. cursor* to detect the exact location of buried nests. Apparently, there are some stimuli released during the end of the incubation period (maybe the increase of sand temperature or sand vibrations) that attract ghost crabs, since the predation was predominant from the sixth week of incubation (Frederico, 2013). Marco et al. (2015) showed similar results, with 80% of predation events starting after 45 days of incubation (Leighton et al 2010). Regardless of how they find nests, they dig a hole through them and feed directly on eggs or buried hatchlings or transport them to other places on the beach. Sometimes, it is possible to find broken shells scattered on the beaches or crab tracks leading to dead turtles (personal observation).

4.4. Climate changes

The predicted climate changes are well-known and several of them are already observable. Environmental effects such as the increase of the global temperature, melting of polar caps and ice sheets, sea level rise, changes in storms frequency and intensity will lead to habitat loss, extinction of species that do not adapt and alteration in species' distribution limits. Such changes will also force some species to alter their ecological features, e.g. phenology, distribution, feeding habits (Hughes, 2000; Witt et al., 2010; Wuethrich, 2000).

Sea turtles as long-migrant ectothermic organisms, highly reliant on several habitats to properly grow and reproduce, are highly susceptible to the effects of climate changes. Nesting beaches will be easily affected by the sea level rise, specially at islands and at areas with intensive coastal constructions (Fish et al., 2008; Mazaris et al., 2009). With the increase of the tide limits landward and coastal erosion, the available habitats will be reduced or even completely lost (Fish et al., 2008, 2005a; Fuentes et al., 2010; Rivas et al., 2016). As a result, the sea turtle nests laid on those beaches will be at great risk of being flooded or eroded and may face some density-dependent problems such as nest destruction by conspecifics, nest infection, and predation may eventually surge (Katselidis et al., 2014; Mazaris et al., 2009). Along with rising sea level, changes in frequency and intensity of storm and precipitation events are expected to happen (Webster et al., 2005), which will eventually intensify the sea level rise effects (Fuentes and Abbs, 2010; Martin, 1996).

In addition to changes in sea level and in atmospheric dynamics, the increase in average air-temperature is another major threat to sea turtles. Sea turtles, as ectothermic and TSD organisms, have several temperature-dependent biological processes, which may be compromised with the increase of temperature (Hawkes et al., 2009). As already mentioned, the incubation process is highly reliant on sand temperature, as well as the clutch sex ratio is dependent on the prevailing temperature of the thermosensitive period (Ackerman, 1997; Carthy et al., 2003; Hawkes et al., 2007; Janzen, 1994b; Matsuzawa et al., 2002; Mrosovsky and Yntema, 1980). With the predicted climate changes, the sex ratio of some populations is expected to be highly skewed towards females or even completely feminized

in extreme cases, or if the sand temperature exceeds the upper thermal limit of embryonic development (33 ºC), (Ackerman, 1997), the clutches may experience high levels of mortality, which will impact negatively the whole population (Hawkes et al., 2007; Matsuzawa et al., 2002). In extreme cases, increasingly female-biased populations may lead to fertilization problems, unfertilized females and total loss of cohorts (Hawkes et al., 2007).

Several reports already showed nesting beaches producing highly female-biased clutches: ≈ 90% for Florida (Hanson et al., 1998; Mrosovsky and Provancha, 1992), North Brazil (Marcovaldi et al., 1997) and Mediterranean rookeries (Godley et al., 2001). Recent studies on Cape Verde population sex ratio show a lower skewed sex ratio than those mentioned above (≈ 79,15% with inter-annual variations; Abella Perez et al., 2016), while South Brazil (57,3% Baptistotte et al., 1999; Marcovaldi et al., 1997), North Carolina (58%, Hawkes et al., 2007), and East Mediterranean populations (60-65%, Kaska et al., 2006) seem to show lower female-biased sex ration. However, with the increase of air temperature, the tendency is to have a more proportion of females.

Furthermore, climate changes consequences may have profound influence the biological features of nesting beaches, by affecting the behavior and distribution of other organisms, such as ghost crabs, possibly altering predator-prey relations as well as a possible influence on colonization capacity of pathogenic microorganisms (e.g. fungus).

5. Study purposes

The Island of Maio, in Cape Verde, is known for its sand coloration variation among beaches, where dark, mixed and light beaches seem to be equally used as nesting beaches (Marco et al., 2013). Previous studies showed that dark sand beaches reach higher thermal conditions (sand albedo, Hays et al., 2001) and consequently are a more severe habitat for nests, by registering higher levels of mortality and more female-biased sex ratio than the lighter ones (Laloe et al., 2014). Considering this, it is plausible to question why do loggerhead continue to nest on such extreme negative beaches, when lighter beaches are available (Marco et al., 2013).

Since the thermal limits of these beaches are higher than on other beaches, it is expected that other temperature-dependent organisms may be affected as well. Ghost crabs (*O. cursor*), other great source of eggs mortality, are highly dependent on sand moisture and very susceptible to water evaporation thus, maybe its density and distribution on those beaches are lower enough to compensate the impact of temperature on nests, justifying the continuing nesting. At the last instance, this behavior just reflects the absence of selection, i.e. the continuous nesting on darker beaches is a result of the philopatry highly present in loggerhead sea turtles.

In order to answer this question, this study set out to understand how external factors influence the reproductive success of loggerhead nesting females, based on possible thermal differences between beaches with different coloration, more precisely the predation and the inundation impact on nest within each beach coloration type. To accomplish the aim of the study, the reproductive success of nesting females was related with the impact of (a) ghost crab predation, (b) ghost crab distribution and density, (c) the inundation phenomena and (d) the temperature effect, among several beaches with different colorations in Maio Island, Cape Verde.

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Chapter 2

Influence of external factors in the survival and reproductive success of the Loggerhead turtle, *Caretta caretta*, in Maio Island, Cape Verde

Abstract

The reproductive success of sea turtles is highly influenced by many environmental and biological conditions of the nesting beach. Sand coloration is highly correlated to sand temperature, with darker sand having higher thermal conditions. On Maio Island there is a great heterogeneity of sand coloration, where sea turtles seem to nest without apparent distinction. Thus, seventy loggerhead turtle nests were monitored in three different beach types (dark, mixed and light sand beaches) to assess the impact of inundation, depredation and temperature on incubation success, as well as the possible interaction between these factors. The hatchery incubation success was also assessed as control. The light sand beaches registered the lowest mortality rate, while dark sand beaches revealed to be the less suitable beach type for nesting due to high temperatures and high predation levels, which lead to the highest mortality rate. The mixed beaches were exceptional by showing the lowest predation rate of all beach types, suggesting that a temperature-extrinsic factor may limit the ghost crab ecology (density and predation).

Key words: sand coloration, reproductive success, *Caretta caretta*, *Ocypode cursor*, thermal impact

Introduction

The scientific community seems to be committed to understand the human-induced impact on ecosystem's health, more precisely on the climatic features of the planet. Considering the trends registered over the last years, climatologists have been trying to predict prospective climatic scenarios , to understand the impact of global warming on several other environmental features, such as oceanic currents, precipitation and storm patterns and sea level rise (IPCC, 2013). Several studies point out that global precipitation will increase, as well as storm intensity and frequency will change globally and regionally (Webster et al., 2005). Also, according to IPCC (2013), during the 20th century, the rate of global mean sea level rise was higher than the rate of the previous two millennia, 1.7 [1.5 to 1.9] mm/yr, and appears to continue to rise (about 3.2 [2.8 – 3.6]mm/yr during the latter period, 1993-2010) (IPCC, 2013). Due to ocean fluctuations (warming and salinity), sea level rise will not be equal around the world, however approximately 70% of the global coastlines are expected to experience a relative sea level change (IPCC, 2013; Nicholls and Cazenave, 2010) for review). As a result, effects such as coastal flooding, saltwater intrusion and long-term coast erosion will occur, and along with direct human impact on these areas (coastal development), it may lead to habitat loss for species dependent on coastal zones (Fish et al., 2005a; Galbraith et al., 2002)

To cope with those predicted novel environmental scenarios, changes in physiology (e.g. metabolic or growth rate), phenology (e.g. migration patterns) or distribution (e.g. habitat shifting toward higher latitudes or higher elevations) are expected to happen in several species (Hughes, 2000). Therefore, it is expected that some species' interactions may be compromised and altered, such as predator-prey or symbiosis relationships, leading to completely alteration of community structure and to some species extinction. Hughes (2000) reviewed some changes already noticed by the scientific community, and the poikilothermic species appear to be particularly susceptible to climatic changes (Ihlow et al., 2012).

The sea turtle, a long-lived and late maturating ectothermic organism, seems to be severely threatened by climate change in several ways (see review Mainwaring et al., 2016; Witt et al., 2010).

The expected increase of temperature represents a major threat to sea turtle survival and reproduction since they are highly dependent on environmental temperature to correctly ensure several vital processes (Ackerman, 1997; Ackerman et al., 1985; Mrosovsky, 1980).

Sand temperature within the nest chamber regulate several reproductive aspects (Hawkes et al., 2009), such as incubation time, proper embryo development (TTR: 33/34 ºC – 25 ºC; Ackerman, 1997), sex determination (Pivotal temperature ≈ 29 ºC; Mrosovsky, 1988; Mrosovsky and Pieau, 1991; Yntema and Mrosovsky, 1982), hatching and emergence success and hatchling fitness (Carthy et al., 2003; Fisher et al., 2014). When the environmental temperature exceeds the lower and upper thermal limits for extended periods, the embryonic development is compromised (Ackerman, 1997; Mcgehee, 1990; Yntema and Mrosovsky, 1982, 1980). And, depending on prevailing temperature, the sex ratio may be balanced (1:1; ≈ 29 ºC) or biased toward one sex, with lower temperatures producing more males and higher temperatures producing more females (Mrosovsky, 1988; Yntema and Mrosovsky, 1982, 1979). Several studies already showed some nesting areas with a skewed sex ratio towards females, which may lead to eventual fertilization problems in the future (Abella et al., 2007b; Hawkes et al., 2007; Hays et al., 2017, 2003; Mrosovsky and Provancha, 1989).

The North East Atlantic subpopulation of loggerhead sea turtle (*Caretta caretta*, Linnaeus 1758), listed as Endangered by the IUCN Red List of Threatened Species (IUCN, 2015) is considered the third largest loggerhead nesting population worldwide and the most endangered of the entire Atlantic (Marco et al., 2011). Cape Verde is considered the main rookery of this subpopulation, hosting more than 95% of all loggerhead nesting activities on the entire eastern Atlantic (8000-30000 nest per year; Martins et al., 2015). In this archipelago situated a *ca.* 500 km from Senegal coast, in West Africa, Boa Vista Island host the majority of nests (≈ 70 - 80% of all nests), while Maio and Sal Islands may represent a great source of productivity by hosting *ca.* 6 to 8% each (Cozens et al., 2011; Martins et al., 2015)

As in other parts of the world, Cape Verde loggerhead population faces several threats that compromise its survival and reproductive success and many of them are a result of anthropogenic impacts. Poaching of female adults and eggs for meat consumption (Marco et al., 2008) and reduction and destruction of nesting beaches by coastal development (including illegal sand extraction activities and tourism development; Taylor and Cozens, 2010) are presented as the main man-induced threats at the nesting sites in Cape Verde (Casale and Marco, 2015; IUCN, 2015) despite the implemented protection laws and the conservation programs in most of the islands (Marco et al., 2012)

Several studies have been conducted to understand the impact of the non-anthropogenic threats such as predation, essentially by *Ocypode cursor* ghost crabs (Frederico, 2013; Marco et al., 2015; Rodrigues et al., 2016; Vieira, 2011) and pathogenic infection (Sarmiento-Ramírez et al., 2014), as well as the impact of predicted climate change (Abella et al., 2007b; Abella Perez et al., 2016; Laloe et al., 2014; Martins et al., 2012) on reproductive success of loggerhead sea turtles (Da Graça, 2011; Varo Cruz, 2010).

Nesting beaches around the world do not experience the same conditions, with diel and seasonal air thermal fluctuations, nest depth, precipitation, vegetation and sand coloration representing great sources of temperature variation within the nest chamber, during incubation (Fisher et al., 2014; Godfrey et al., 1996; Hawkes et al., 2009; Hays et al., 2001; Janzen, 1994a; Kamel, 2013; Matsuzawa et al., 2002; Morreale et al., 1982; Mrosovsky, 1988; Mrosovsky et al., 1984). Beaches with light, mixed or dark sand coloration can be found in Maio Island where loggerhead sea turtles seem to nest without apparent distinction (Marco et al., 2013). Sand coloration appears to be highly correlated with sand

temperature (sand albedo, Hays et al., 2001) with darker sand beaches should have higher thermal limits than the lighter ones. Since temperature directly affects the reproductive success of sea turtles, different thermal conditions may result in different reproductive successes. Furthermore, different temperatures limits may affect differently the ecology (e.g. behavior and distribution) of other organisms, such as ghost crabs, possibly altering predator-prey relations as well as may affect the colonization capacity of pathogenic microorganisms (e.g. fungus, Sarmiento-Ramírez et al., 2014, 2010).

Considering that the main eggs and hatchlings' predator in Cape Verde – ghost crab – is an ectothermic organism, highly dependent on gills moisture and highly susceptible to water loss by evaporation, it is expected that darker beaches, with higher sand temperature limits and higher rates of evaporation, are more severe habitats than lighter sand beaches, and as a result, the ghost crabs distribution and density would be limited and the predation impact would be lower on those beaches.

This study aims for a better understanding of the impact of sand coloration of nesting beaches on the reproductive success of loggerhead sea turtles. For that, the reproductive success of the turtles was related to (a) the abundance and distribution of *O. cursor* and its predation impact on nests; (b) the impact of flooding events on nests and (c) the sand temperature for beaches with different sand coloration. Understanding the impact of sand coloration (and its temperature) on reproductive success of sea turtles and on the external factors that affect it, may help to understand the reason for which the nesting females continue to nest on potentially lethal thermal beaches and eventually may help to improve the management decisions of this important rookery, considering the predicted climate change.

Material and Methods

Study area

The Cape Verde Archipelago is located *ca.* 500 km west of the Senegal coast and is comprised by 10 volcanic islands and some islets (Figure 2.1). It is characterized by a tropical dry climate with arid and semiarid climatic conditions mainly due to the Sahel region (transitional region between the Sahara Desert and moist tropical climates). The study period coincided with the nesting season (mid-July to mid-October), including the rainy months of the warm season (August to October).

Seven beaches located on the eastside of the island with distinct geomorphological features and anthropogenic impacts were selected. Considering the purpose of the study, these seven beaches were grouped according to their sand coloration: three light sand beaches (Prainha, Praiona and Boca Ribeira); two mixed sand beaches (Ribeira Baia e Calheta Dama) and two dark sand beaches (Pajoana and Monte Branco). All beaches were pristine and with low and infrequent anthropogenic impact, with fishing being the most common activity in most of the beaches. Ribeira Baia was the beach with higher fishing activities. Also, all beaches were characterized by supralittoral dunes.

Field study of Ghost crabs (*Ocypode cursor*)

The abundance and distribution of ghost crabs in different types of beaches were estimated using the indirect method of burrow counting. Transects of 2 meters wide were randomly placed along the sea-to-dune axis, from the high tide line to the supralittoral dune zone. The intertidal zone was not included since there are no nesting activities there. The length of transects depends on high tide amplitude and beach slope and was always recorded in order to estimate the transect area and available habitat. All transects were done in the first 2 hours after sunrise. The sampling was recorded with an average 5 days of interval. The number of transects per beach varied according to beach size and the

distance between transect was average 25 meters. There were placed 9 transects in Praiona; 7 in Boca Ribeira; 6 in Prainha e Calheta Dama and 5 in Ribeira Baia, Monte Branco and Pajoana.

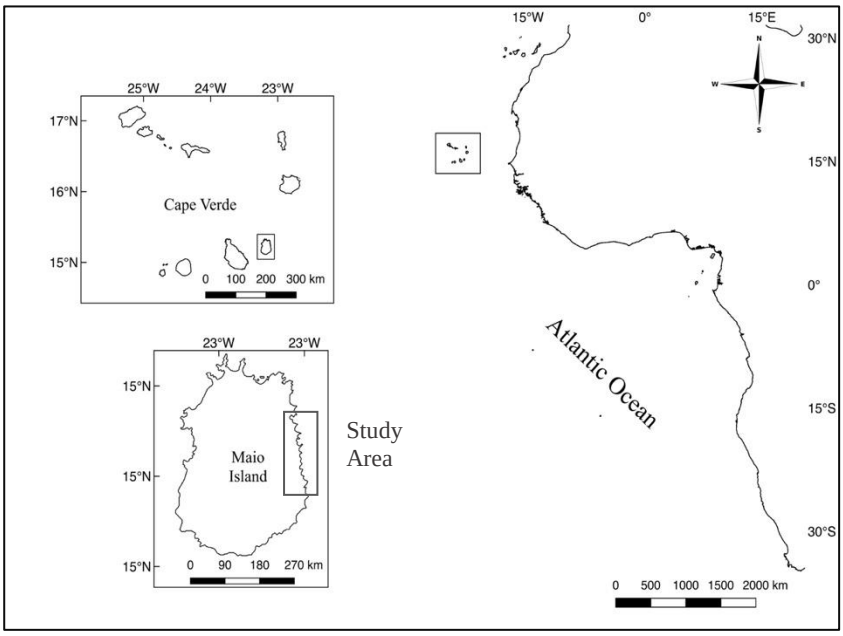

Figure 2.1. Maps of archipelago of Cape Verde, Maio Island and the study area (seven beaches).

In each transect, the number of burrows was counted and its size was measured with a scale of 15 centimeters (± 0,1 cm). The mean burrow size allowed to estimate the mean ghost crab size, since this two measures are highly correlated (Marco et al., 2015). The ghost crab relative abundance was estimated based on the counting of burrows, while for the mean relative density the number of burrows counted was divided by the area of the transect. This last measure accompanies the variability of the available habitat and considers the size of the beach. These three measures allowed to evaluate the distribution of ghost crab along the tide-dune axis (intra-transects), along the beach (inter-transects) and between different beaches.

Reproductive success of loggerhead sea turtle (*Caretta caretta*)

To evaluate the reproductive success and to understand the impact of external factors on it, 70 nests (10 nests per beach) were monitored since the day of oviposition until the end of incubation. In the majority of nests, the oviposition was observed and the number of eggs was counted at the moment. For a few number of nests, the oviposition was not observed and the eggs' count implied the excavation of the nest. In this case, only nests with a maximum of 6 hours after oviposition were included in this study. The period after oviposition was known due to frequent nocturnal patrol of the beaches. The counting of exhumed eggs was taken with very caution, avoiding rotation movements.

All nests were marked by triangulation and the date and hour of oviposition, beach name, the number of eggs and GPS location (Garmin etrex10; error ± 3 meters) were registered. The nests were monitored daily and every alteration of the nest conditions was recorded: inundation and erosion phenomena (loss or gain of sand, water runoff, submersion, partial inundation, total dragging to the sea); ghost crab predation events (number and size of the holes); predation events from other species; human impact (stolen eggs; nest excavation attempts); emergence events (number of hatchlings or trails). After registration, all predation signals were erased to avoid double counting. Predated nests were considered as any nest with ghost crab evidence and inundated nests were considered all nests that were prone to some inundation phenomena at least once during incubation. In this study, only nests with holes larger

than two centimeters were considered predated, since these holes are from potential eaters of eggs and hatchlings (Frederico, 2013)

The incubation period corresponded to the number of days elapsed between oviposition and emergence. The exhumation was carried on 5 days after the last big emergence or at the end of 60-65 days of incubation if no evidence of emergence were observed. The number of (a) dead or alive hatchlings within the nest, (b) hatched eggs shell, (c) dead or alive pipped hatchlings and (d) unhatched eggs were counted. The unhatched eggs were classified according to their development stage and predated and non-predated eggs were distinguished. Broken shells and small pieces were counted as a shell only if their sum corresponded to, at least, ¾ of an entire egg. Alive pipped hatchlings within the nest were considered hatched eggs, along with dead or alive hatchlings, but dead pipped hatchlings were categorized as unhatched eggs.

Nesting success was calculated by dividing the number of nests by the number of nesting activities. Hatching success was calculated by dividing the sum of hatched shells and alive pipped hatchlings (hatched eggs) by the clutch size. Emergence success was calculated by subtracting the number of hatchlings within the nest to the number of egg shells and dividing this number by the clutch size.

The variation of the egg number during incubation was calculated by subtracting the number of eggs in exhumation to the number of eggs in oviposition. This variation resulted from the counting error during oviposition and from the eggs stolen by ghost crabs in natural nests. At the hatchery, the eggs variation was only due to counting error during the translocation. The average of eggs variation within a group allows to eliminate the counting error, thus in natural nests, this difference was considered the number of stolen eggs. Considering that the clutch size was not always counted correctly in oviposition, the real clutch size was considered the highest value counted.

The mortality rate included every source of death and resulted from the sum of unhatched eggs, predated eggs, dead pipped hatchlings and dead hatchlings within the nest divided by the clutch size. The predated eggs included shells and unhatched eggs with predation evidence and the stolen eggs. The mortality rate was subdivided into two rates according to the mortality source. The mortality by predation, or the predation rate, included all kind of predation-induced mortality (was calculated by subtracting the hatched eggs, the dead pipped hatchlings and the unhatched unpredated eggs to the clutch size, and then dividing by the clutch size). The second rate, referred as mortality by other causes, reflects the impact of other mortality causes such as temperature, fungal or bacterial infections, desiccation, that are difficult to determine during exhumation: the sum of the unhatched eggs, the dead pipped hatchlings and the dead hatchlings divided by the clutch size. Also, the embryonic mortality rate was estimated by subtracting the hatched eggs (dead or alive hatchlings and alive pipped hatchlings) to the total clutch size and then dividing that number by the clutch size.

Nests killed by inundation phenomena (flooded or washed away) were not attacked by ghost crabs or other sources of predation, with flooding being the only source of mortality. Thus, to obtain more accurate results concerning the impact of predation and other causes, those nests were excluded when averages were calculated.

In addition, 23 nests were translocated to the light sand hatchery (see translocation procedure in Marco et al., 2015), in controlled conditions where factors such as predation, erosion and inundation were non-existent. All causes of mortality in these nests resulted from “other causes” than predation,

such as those mentioned above. The methodology for natural nests described above was applied to the hatchery nests and all rates were calculated, when applicable.

Temperature evaluation

Sand temperature was evaluated on three different nests, two nests in dark beach (PV19 and PV50) and one nest in the hatchery (A7). Were used five automatic temperature data loggers (TidbiT Onset, *http://onsetcomp.com*, accuracy of ± 0.3 ºC) in each nest, programmed to record temperature in every 30 minutes: one at the bottom of the nest within the first eggs, one at the center, one at the periphery of the nest at the same depth of the second one and one at the top. Plus, one more was placed 1 meter away of the nest and at the same central depth, as a control effect.

Statistical methods

The statistical analysis was carried out through the SPSS *Statistics* 2.3 software. The emergence and hatching success as well as the mortality rates were arcsin square root-transformed to obtain more normal and homoscedastic data, however non-parametric analysis was carried out due to the continuing absence of normality and homoscedasticity of the variances: Kruskal-Wallis test was carried out to analyze each rate as well as the abundance, density and size of ghost crab's holes as well as to analyze the successes and mortality rates between the three beach types (different sand coloration) and the seven studied beaches; Mann-Whitney test was used to compared the differences between two treatments; and the Chi-square test (and the Fisher's exact test) was performed to analyze differences in predated and inundated nests among beach types and individual beaches. The temperature analyzes were carried out following the same previous procedures (non-parametric tests) due to the absence of normality and homoscedasticity.

Results

Field Study of Ghost crabs

In general, the majority of sampled holes corresponded to small holes (with less than 2 centimeters), with only an average 10.48% of them belonging to large holes (with 2cm or above).

The dark beaches revealed the greatest mean density of small (0.3812, SD ± 0.3163) and large holes (0.0523, SD ± 0.0511), statistically different from the light beaches (Mann-Whitney: small holes U = 9290.0, p = 0.026; large holes U = 9256.5, p = 0.019). Only the small hole's density of dark sand beaches revealed to be similar to the density value of mixed beaches (Mann-whitney: U = 5122.0, p=0.390). The light and the mixed beaches revealed both lower density values (Table 2.1), similar to each other (Mann-whitney: small holes U = 11242.0, p = 0.293; large holes U = 11232.5, p = 0.264).

Among all seven beaches, Prainha, Pajoana and Calheta Dama were the ones with the lowest density of small holes (Pnha: 0.2311 holes/m^2, SD ± 0.2035; PJ: 0.2742 holes/m^2, SD ± 0.2083; CD: 0.2874 holes/m^2, SD ± 0.2686) while Monte Branco stood out for its high-density value (MB: 0.4882 holes/m^2, SD ± 0.3681). Regarding to the large holes, Calheta Dama and Prainha were again the beaches with the lowest density (CD: 0.0295 holes/m^2, SD ± 0.0445; Pnha: 0.0261 holes/m^2, SD ± 0.0348) while, Pajoana revealed a high density of large hole, along with Monte Branco and Boca Ribeira (BR: 0.05275 holes/m^2, SD ± 0.0560, PJ: 0.05245 holes/m^2, SD ± 0.0433, MB: 0.0521 holes/m^2, SD ± 0.0521).

Regarding to the size of crab holes, there were also significant differences between beaches (Kruskal-Wallis: χ_6^2 = 28.959, p = 0.000) and between beach types (Kruskal-Wallis: χ_2^2 = 23.477, p =

0.000; Table 2.1). Although the light beaches showed lower ghost crab density than the dark beaches, it showed the highest hole size (3.46 cm, SD ± 0.99, 2.0 – 6.0 cm), significantly different from the dark (3.05 cm, SD ± 0.77, 2.0 – 5.0 cm; Mann-whitney$_{light\text{-}dark}$: U = 13408.0, p < 0.001) and from the mixed beaches (2.99 cm, SD ± 0.75, 2.0 – 6.0 cm; Mann-whitney$_{light\text{-}mixed}$: U = 9619.0, p < 0.001). The mixed and dark beaches revealed similar values (Mann-whitney$_{mixed\text{-}dark}$: U = 7375.0, p = 0.515).

Praiona was the beach with the highest mean hole size (3.62 cm, SD ± 1.13, 2.0 – 6.0 cm), along with the two other light sand beaches (Prainha: 3.45 cm, SD ± 0.99, 2.0 – 6.0 cm; Boca Ribeira: 3.29 cm, SD ± 0.82, 2.0 – 5.5 cm). Pajoana and Ribeira Baia registered the lowest average of hole size (2.95 cm, SD ± 0.76, 2.0 – 5.0 cm and 2.94 cm, SD ± 0.71, 2.0 – 4.5 cm, respectively).

Table 2.1. Average density and size variables of ghost crab holes for each individual beach and each beach type (dark, mixed and light sand beaches). Mean (± Standard deviation). Distinct letters and numbers (in uppercase) denote statistical differences between treatment, at the 0.05 confidence level. N_1 presents the number of all transects sampled per treatment; N_2 presents the number of large holes (≥2cm diameter) sampled in all transects per treatment

	N_1	Total Density	Density of small holes (<2cm)	Density of large holes (≥2cm)	N_2	Hole's size
Monte Branco	50	0.5403 (± 0.3870)	0.4882 (± 0.3681)	0.0521 (± 0.0585)^{2,3}	73	3.15 (± 0.76)
Pajoana	50	0.3267 (± 0.2219)	0.2742 (± 0.2083)	0.0525 (± 0.0433)^{3}	69	2.95 (± 0.76)
Calheta Dama	60	0.3169 (± 0.2808)	0.2874 (± 0.2686)	0.0295 (± 0.0445)^{1}	40	3.08 (± 0.82)
Ribeira Baia	50	0.4596 (± 0.3590)	0.4190 (± 0.3443)	0.0405 (± 0.0505)^{1,2}	69	2.93 (± 0.71)
Boca Ribeira	70	0.4187 (± 0.2855)	0.3659 (± 0.2716)	0.0528 (± 0.0560)^{2,3}	97	3.29 (± 0.82)
Prainha	60	0.2572 (± 0.2104)	0.2311 (± 0.2035)	0.0261 (± 0.0348)^{1}	47	3.45 (± 0.98)
Praiona	90	0.4246 (± 0.6619)	0.3827 (± 0.6481)	0.0419 (± 0.0516)^{1,2}	98	3.62 (± 1.13)
Dark beaches	100	0.4335 (± 0.3317)^{A}	0.3812 (± 0.3163)^{A}	0.0523 (± 0.0511)^{A}	142	3.05 (± 0.77)^{A}
Mixed beaches	110	0.3817 (± 0.3252)^{AB}	0.3472 (± 0.3109)^{AB}	0.0345 (± 0.0474)^{B}	109	2.99 (± 0.75)^{A}
Light beaches	220	0.3771 (± 0.4702)^{B}	0.3360 (± 0.4575)^{B}	0.0411 (± 0.0500)^{B}	242	3.45 (± 0.99)^{B}
Global	430	0.3914 (± 0.4070)	0.3494 (± 0.3935)	0.0420 (± 0.0499)	493	3.24 (± 0.91)

Nest survey

During the night patrol season, 2714 nesting activities were recorded between the seven monitored beaches, of which 1288 (47,46%) were nests: 668 nest activities occurred in dark beaches, 1200 in mixed beaches and 846 in light sand beaches. The nesting success revealed to be dependent on beach (chi-square test: χ_6^2 = 107.23, p=0.000) and on beach types (chi-square test: χ_2^2 = 84.22, p=0.000).

The dark sand beaches showed the lowest nesting success and the lowest nest density (38.57%, SD ± 6.52 and 0.27 nests/m^2, SD ± 0.09, respectively). In fact, the dark sand beaches registered lower number of nests than the expected per beach area and per nesting activities (Table 2.2), suggesting a possible environmental pressure that conditions the nesting success. Light beaches revealed intermediate values of nesting success and nesting density, very similar to those expected by the Chi-square tests (Table 2.2), while mixed beaches stood out for their high value of nest density (1.25 nests/m^2, SD ± 0.83) and nesting success (52.5%, SD ± 7.55), which was at least 20% higher than expected.

Table 2.2. Nesting information about the seven monitored beaches and the three beach types (dark, mixed and light beaches). Mean (± Standard deviation). *Global values are average values. Boxes includes information about chi-square test results per each treatment (beach n =7 and beach type n = 3). Symbolic system was applied to understand the variation of the observed values comparing to the expected ones: observed values were higher than 50% (++), more than 20% higher (+); within a range of 20% (=); at least 20% lower (-) or lower than 50% (--) the expected values.

Beach	Beach Area (m^2)	Nesting activities	Number of nests	Nest density (n/m^2)	Nesting success	Expected nests by beach area		Expected nests by nesting activities	
MB	592	580	197	0,333	33.97%	259.71	-	269.8	-
PJ	190	88	38	0.200	43.18%	75.05	-	66.5	-
CD	316	441	208	0.658	47.17%	172.48	+	205.1	=
RB	239	759	439	1.837	57.84%	223.17	+	353.0	+
BR	361	358	152	0.421	42.46%	168.86	=	166.5	=
Pnha	314	264	139	0.443	52.65%	149.11	=	122.8	=
Pona	613	224	115	0.188	51,34%	239.63	--	104.2	=
		2714	1288	0.583*	46.94%*	χ^2 = 472.04 df = 6 p < 0.001		χ^2= 107.23 df = 6 p < 0.001	
Dark beaches	782	668	235	0.266 (± 0.094)	38.57% (± 6.52)^A	395.65	-	336.3	-
Mixed beaches	555	1200	647	1.248 (± 0.833)	52.50% (± 7.55)^B	557.60	+	558.2	+
Light beaches	1288	846	406	0.350 (± 0.141)	48.82% (± 5.55)^C	1288.00	--	393.5	=
		2714	1288	0.583*	46.94%*	χ^2 = 343.78 df = 2 p < 0.001		χ^2 = 84.22 df = 2 p < 0.001	

Of the 70 studied nests, 52.86% were prone to inundation phenomena at least once during incubation, of which 29.72% died due to this cause, which represents 15.71% of all monitored nests. Among beach types, the number of nests subject to inundation events revealed to be independent of the sand coloration (chi-square test: χ_2^2 = 5.991, p = 0.050, n=70) but not independent of the beach (chi-square test: χ_6^2 = 20.359, p = 0.002, n=70) (Table 2.3). As well as, the number of nests killed by inundation events showed no association between beach types (chi-square test: χ_2^2 = 0.917, p = 0.632, n=70) but varied between beaches (chi-square test: χ_6^2 = 14.884, p = 0.002, n=70)(Table 2.3).

Pajoana's beach, a short and narrow beach, limited by vegetation and a lagoon, had all nests flooded at least once during incubation period, yet only 30% of the nests died due to that (n=10). Although Praiona and Monte Branco registered 5 and 3 inundated nests, respectively, none suffered lethal events. Ribeira Baia and Prainha registered 5 (n=10) and 7 (n=10) of flooded nests, respectively, though only one in each beach died due to sand erosion caused by rain-induced water streams. Boca Ribeira was the beach with the highest mortality by inundation: five of the six flooded nests were washed away into the sea by brook streams. All 5 nests were in the same stream-affected area, along with other non-monitored nests that were washed away into the sea as well.

Not all inundation events resulted in nest death. In fact, 70.27% of the flooded nests (n=37) were essentially subjected to high tides swash and did not die because of it. The mean hatching success of hatched nests that were prone to at least one inundation event was 43.60% (SD ± 24.70%, 6.25 – 85.71 %, n = 20).

Table 2.3. Results from nests monitoring during the nesting season on the seven studied beaches in Maio Island (Cape Verde) and the three beach type (dark, mixed and light beaches). Percentage % (number of nests). Distinct letters (for beach type) and number (for beach) denote the statistical differences between groups as a result of the Chi-square test at the 0.05 confidence level (α).

	No. of flooded nests	**No. of nests killed by inundation events**	**No. of predated nests**	**No. of fully predated nests**
Global	52.86% (37)	15.71% (11)	67.80% (40)	10.17% (6)
Dark beaches	65% (13)	15% (3)	82.35% (14) ^{A}	20% (4) ^{A}
Mixed beaches	30% (6)	10% (2)	44.44% (8) ^{B}	0% (0) ^{B}
Light beaches	60% (18)	20% (6)	75.00% (18) ^{A}	6.67% (2) ^{AB}
Monte Branco	30% (3)^{2,3}	0% (0)^{1}	70% (7)^{1,2}	10% (1)
Pajoana	100% (10)^{1}	30% (3)^{2}	100% (7)^{1}	42,86% (3)
Calheta Dama	10% (1)^{3}	10% (1)^{1,2}	22.22% (2)^{2}	0% 0
Ribeira Baia	50% (5)^{1,2,3}	10% (1)^{1,2}	66.67% (6)^{1,2}	0% 0
Boca Ribeira	60% (6)^{1,2,3}	50% (5)^{2}	40.0% (2)^{2}	0% 0
Prainha	70% (7)^{1,2}	10% (1)^{1,2}	66.67% (6)^{1,2}	0% 0
Praiona	50% (5)^{2,3}	0% (0)^{1}	100% (10)^{1}	20% (2)

The ghost crab was the only predator found predating the sea turtles' nests, with zero nests being directly affected by human action or other predator species. Overall, 67.80% of the 59 nests assigned to predation analysis were attacked by ghost crabs, at least once during incubation period, with 15.0% of them being fully predated with no eggs left (10.2% of all studied nests, n = 59 nests)(Table 2.3). A significantly lower proportion of predated nests were found (chi-square test: χ_2^2 = 6.716, p = 0.035, n = 59 nests) on the mixed sand beaches (44.44%, n = 18 nests), comparing to the dark beaches (82.35%, n = 17 nests) and light beaches (75.0%, n = 24 nests). No differences in proportions were found between dark and light beaches.

All nests in Praiona and Pajoana suffered predation (n = 10 and n = 7, respectively), while Calheta Dama and Boca Ribeira revealed the lowest record of predated nests (22.22%, n = 9 and 40.0%, n= 5, respectively; Table 2.3). Only Monte Branco, Pajoana (both dark sand beaches) and Praiona (light sand beach) registered fully predated nests (Table 2.3).

The hatchery nests registered the lowest mean variation of eggs number of all treatments, nearly zero (0.73 eggs, SD ± 2.83, n=23), suggesting that the counting error can be eliminated when carried out a group average. Considering this, it is possible to affirm that the average of the variation of eggs number of natural nests' groups is due to eggs stolen by ghost crabs. No significant differences were found between the hatchery and the mixed beaches' mean number of eggs (4.50 eggs, SD ± 9.39, n = 18, 0 to 24 eggs; Mann-whitney: U = 149.0, p = 0.178) who recorded the lowest value of the three beach types. On the other hand, the hatchery's mean variation was significantly different from the light beaches (21.67 eggs, SD ± 28.75, n = 24, 0 to 86 eggs; Mann-whitney: U =107.5, p = 0.001) and from the dark beaches (35.82 eggs, SD ± 32.32, n = 17, 0 to 83 eggs; Mann-whitney: U = 28.0, p = 0.000), indicating that the number of stolen eggs were significantly higher in dark and light beaches than in mixed beaches.

Only Calheta Dama (2.56 eggs, SD ± 10.25 eggs) and Ribeira Baia (6.44 eggs, SD ± 8.59 eggs), where predation was low, recorded a similar mean variation of eggs number to the hatchery (Figure 2.2). Pajoana stands out for recording the highest mean variation during incubation (56.43 eggs, SD ± 30.57 eggs), only similar to Praiona (34.50 eggs, SD ± 31.03 eggs; Mann-Whitney: U = 21.0, p = 0.172), both with great predation record.

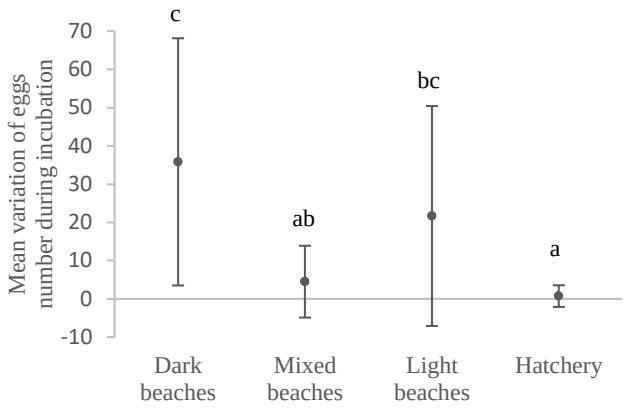

Figure 2.2. Mean variation of eggs number during incubation for dark (n= 17), mixed (n=18) and light beaches (n=24) and for the hatchery (n=23). The eggs number variation in natural nests was resulted from the counting error during oviposition and eggs stolen by crabs during incubation, while in the hatchery the variation of eggs number during incubation was only due to counting error. The error bars represent the standard deviation (SD). Distinct letters represent significant differences between treatments, as a result of the non-parametric Kruskal-Wallis test, at the 0.05 confidence level (α)

The hatchery's nests revealed a significantly lower mean mortality rate than any group of natural nests (beach types: Kruskal-Wallis χ_3^2 = 36.856, p = 0.000; beaches: Kruskal-Wallis: χ_7^2 = 41.484, p = 0.000) (Figure 2.3; Table 2.4). The dark sand nests recorded the highest average mortality rate (78.91%, SD ± 21.27%, n=17, 32.1-100%), significantly different from the light sand nests (53.72%, SD ± 27.90, n =24, 4.3-100%; MW: U = 100.5, p = 0.006) and the mixed sand nests (57.47%, SD ± 22.40%; Mann-whitney: U = 77.0, p = 0.012). The light beaches recorded a similar overall mortality rate to mixed beaches (Mann-whitney: U = 195.5, p = 0.602).

Table 2.4. Mean values of the main variables analyzed for each beach type (n = 59 nests) and for the hatchery (n = 23 nests). Standard deviation in parenthesis. Distinct letters denote significant differences at the 0.05 level as a result of non-parametric Kruskal-Wallis test. *Statistically significant.

	Clutch Size	**Variation of eggs number***	**Hatching Success***	**Mortality rate***	**Mortality by other causes rate***	**Mortality by predation rate***
Dark beaches	79.30 (±11.60)	35.82 (±32.32)^{C}	21.53% (± 22.33)^{A}	78.91% (± 21.27)^{C}	25.70% (± 30.54)^{A}	53.21% (± 39.27)^{C}
Mixed beaches	88.65 (±17.06)	4.50 (±9.39)^{AB}	43.88% (± 22.59)^{B}	57.47% (± 22.40)^{B}	49.95% (± 23.59)^{B}	7.52% (± 8.81)^{A}
Light beaches	85.27 (±12.43)	21.67 (±28.75)^{BC}	47.20% (± 28.16)^{B}	53.72% (±27.90)^{B}	25.30% (± 24.50)^{A}	28.42% (± 33.60)^{B}
Hatchery	77.91 (±14.24)	0.73 (±2.83)^{A}	76.23% (± 14.18)^{C}	24.06% (± 14.15)^{A}	24.06% (± 14.15)^{A}	-

The impact of predation and other causes varied between beach type (Figure 2.3). The predation revealed to be the major source of mortality in dark beaches **(**Kruskal-Wallis: χ_1^2 = 5.094, p = 0.024), representing 67.43% of all eggs mortality there (53.21%, SD ± 39.28, n = 17, 0-100%), while other causes only contributed with 32.57% to eggs mortality (25.70%, SD ± 30.54, n = 17, 0-100%).

On the other hand, although light and mixed beaches recorded similar mortality rates, the impact of each cause on each beach type differed (Figure 2.3): on light beaches, the predation and other causes had similar percentage (other causes: 25.30%, SD ± 24.50 vs predation: 28.42%, SD ± 33.82, n = 17; Kruskal-Wallis: χ_1^2 = 0.047, p = 0.828) while, on mixed beaches other causes than predation revealed to be the major cause of mortality (other causes: 49.95%, SD ± 23.59 vs predation: 7.52%, SD ± 8.81, n = 18; Kruskal-Wallis: χ_1^2 = 24.737, p = 0.000).

In fact, the mixed beaches revealed the highest mean mortality by other causes, significantly different from the light beaches (Mann-whitney$_{mixed\text{-}light}$: U= 97.5, p=0.003), the dark beaches (Mann-Whitney$_{mixed\text{-}dark}$: U= 77.5, p=0.012) and the hatchery (Mann-Whitney$_{mixed\text{-}hatchery}$: U= 76.0, p=0.001), which were similar among them (Mann-Whitney$_{light\text{-}dark}$: U = 179.5, p = 0.514; Mann-Whitney$_{light\text{-}hatchery}$: U = 248.0, p = 0.551; Mann-Whitney$_{hatchery\text{-}dark}$: U = 169.0, p = 0.467) (Table 2.4).

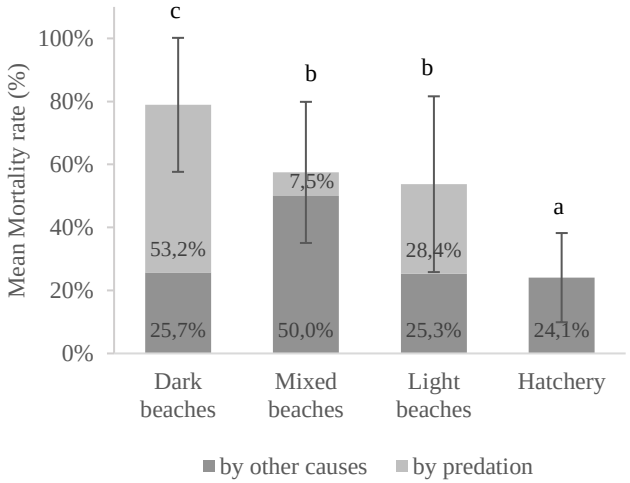

Figure 2.3. Mean mortality rate of the three beach types: dark (n=17), mixed (n=18) and light (n=24) beaches. Each bar comprises the impact of predation (light grey) and the impact of other causes (dark grey) on overall mortality. Note that the mortality rate at the hatchery's nests only includes other causes than predation, since no predation events were registered there. The letters represent the statistical differences of global mortality between treatments, resulted from the non-parametric Mann-Whitney test. The error bars represent the standard deviation of mean overall mortality rate.

Temperature assessment

In the three studied nests, the sand temperature reached, at some point of incubation, the maximum thermal limit (≈33ºC), with dark sand nests (PV19 and PV50) being the first ones to achieve it, right at the first third of incubation. (Figure 2.4)

PV19 recorded the highest mean temperature (33.32 ºC, SD ± 1.19, 27.14 – 37.15 ºC), with the hottest values recorded on the middle third of incubation. The light sand hatchery nest (A7) registered the lowest mean sand temperature (32.55 ºC, SD ± 1.37, 29.87 – 34.62 ºC). From the middle third of incubation, there is an evident temperature increase within the nest, comparing to the constant control temperature outside the nest, due to metabolic heat (Figure 2.4). PV50, although in dark sand, registered values closer to the hatchery's values than the other dark sand nest (32.61 ºC, SD ± 1.35, 27.73 – 34.86 ºC), mainly because this nest was constantly prone to swash effect of the high tide and was easily flooded by intensive high tides.

The precipitation and inundation events resulted in temperature momentary decrease within the nest. From the September 12th, both natural nests (PV19 and PV50) suffered abrupt decreases of temperature due to frequent and intensive periods of rain and inundation by energetic high tide waves (Figure 2.4).

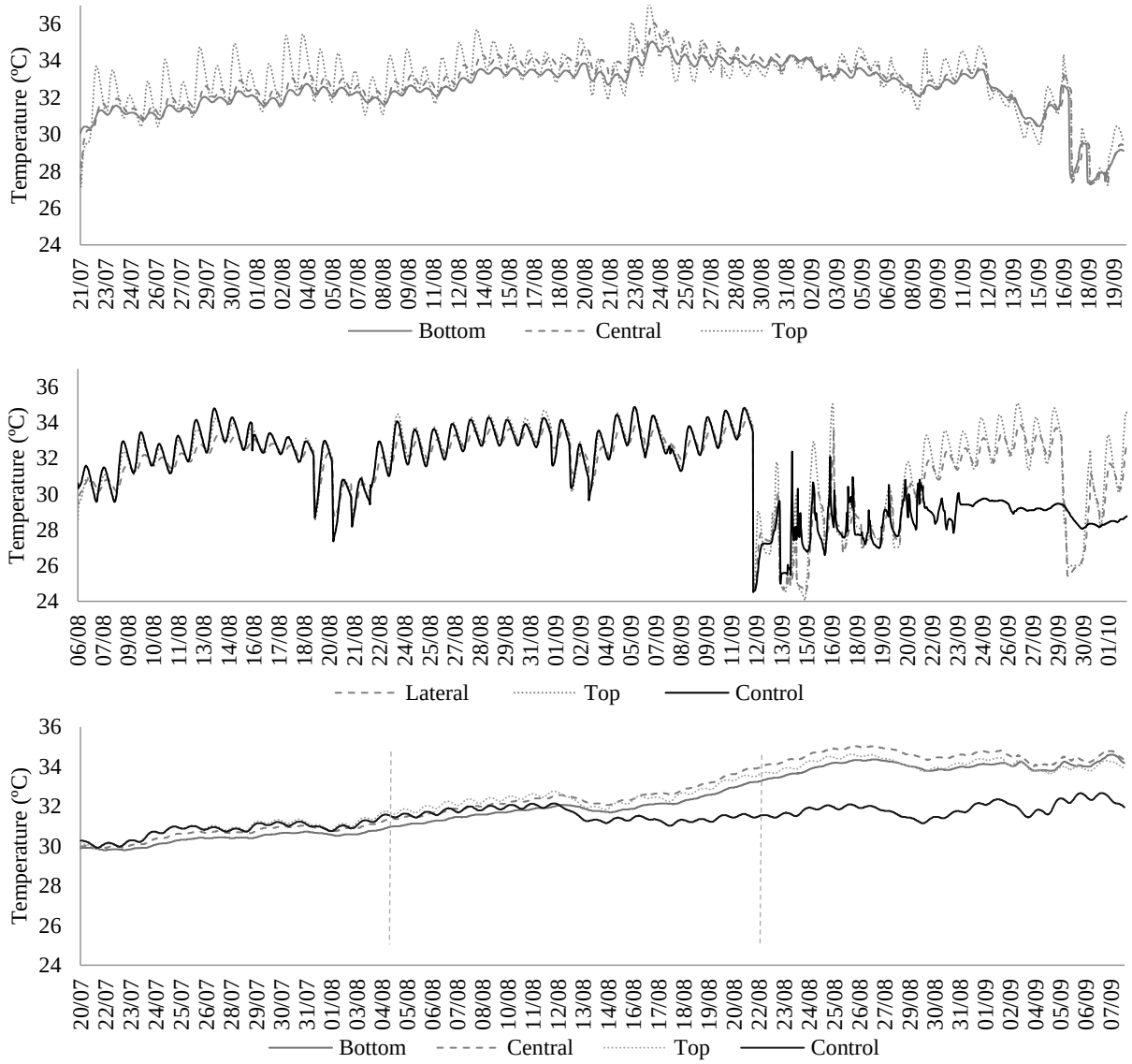

Figure 2.4. Incubation temperature for (A) PV19; (B) PV50, both dark sand nests and (C) A7, a hatchery's nest. Bottom - data logger placed at the bottom of the nest; Central - data logger placed at the center of the nest; Lateral - data logger placed at the periphery (same depth of center logger); Top – data logger placed at the top of the nest; Control – data logger placed 1 meter away of the nest, at the center depth. The doted vertical lines represent the limit between thirds of incubation.

Discussion

Of all assessed groups, the hatchery registered the highest hatching success (on average 50% greater than the hatching success *in situ)* and, consequently, the lowest mortality rate, revealing to be the most effective and productive place for the development of sea turtles' embryos. Although the translocation of nests to the hatchery is highly associated with jerking and egg rotation issues which can lead to eggs' death, it has been shown to be a very beneficial technique for the reproductive success of *Caretta caretta* around the world (Marco, 2015; Abella et al., 2007), by reducing some mortality causes such as natural predation and inundation.

There was a similar impact of mortality by other causes between light sand natural nests and light sand hatchery nests, with the predation impact on natural light beaches being the main reason that distinguishes those two treatments. Thus, it is plausible to assume that light beaches are inevitably the more suitable beach type to implement a hatchery.

The inundation impact on nests varied among beaches, essentially due to topography (e.g. width and slope) and sand accretion-erosion dynamics. The location of the nest in relation to the high tidal range and to the potential rain-induced water streams will reflex the propensity, frequency and intensity of the flooding events. During this study, more than a half of the nests suffered inundation at least once, but only 15.71% of them were actually killed by it. The remain partial flooded nests showing an average of 43% of hatching success, suggesting that short and sporadic events do not lead to entire clutch death. In fact, it can favor incubation by reducing for instants the sand temperature within the nest, as noted in the temperature log.

With the sea level rise, currently suitable nesting beaches may lose a great portion of their available habitat, leading to density-dependent problems (Katselidis et al., 2014). Nest inundation events will increase in frequency and intensity due to the sea agitation intensification (tide amplitude, waves energy, etc.) and the storms effect (Fish et al., 2008, 2005b; Fuentes et al., 2010; Pike et al., 2015; Rivas et al., 2016).

There was a great inter-beach variability of mean mortality by other causes, ghost crab predation impact and ghost crab density, mainly due to their different environmental features (topography, hydrodynamics, sediment properties, vegetation, etc.). However, some patterns were found between beach types. As expected, the dark sand beaches registered higher values of mean sand temperature (due to sand albedo) and higher eggs' mortality rate. Based on this, on the one hand, it was also expected that mortality by other causes was substantially higher in dark sand beaches than in the other beach types, as a consequence of temperature negative impact. On the other hand, it would be expected a lower predation rate on those beaches, since the ecology of ghost crabs could be affected by the severe thermal conditions there. These two last hypotheses weren't verified: the dark sand nests were equally affected by other causes (such as temperature,) as the light sand nests and, in opposition to what was expected, the density of ghost crabs revealed to be statistically superior on those dark beaches, comparing to the other beach types. It would also be expected that mixed sand beaches obtained intermediate results, both in temperature and in ghost crab impact. However, this study showed that those beaches registered on average the lowest density of ghost crabs and the lowest ghost crab predation rate of all beaches.

These results suggest that, although ghost crabs are highly reliant on gills moisture and reveal temperature conditioned-behaviors (e.g. crepuscular activity, deep holes close to water table, etc.), these organisms do not seem to respond to the different thermal conditions of the beaches. In fact, they seem to prosper in warmer environments. It also suggests that some environmental pressure, especially present on mixed sand beaches, seem to limit the density of the large crabs and their predatory activity, which justify the lowest large crab's density and the lowest predation impact on loggerhead turtle nests. Several environmental features can be pointed out as the reason of these results. It has been shown the predation impact on sea turtles nests are related with the density of the predators, with denser beaches having more predated nests (Marco et al., 2015; Vieira, 2011), similar to what happened in this study.

How ghost crab (Ocypode genus) find buried sea turtle nests is not quite explicit, but their acute senses of smell, hearing and vision (Lucrezi & Schlacher, 2014) may allow them to detect temperature variations of the sand, hatchlings vibration during hatching or the nest smell (Horch, 1971; Lagerspetz and Vainio, 2006), which explain why the majority of ghost crab attacks only start at late periods of incubation (Frederico, 2013; Marco et al., 2015). Maybe the sand composition of mixed beaches has particular qualities that camouflage the nests in some way, making it difficult to detect, which justify the low predation rate in some intermediate crab density beaches.

Barton & Roth (2006) have shown the importance of ghost crabs' predators, such as raccoons, in controlling the density and the predation impact of these crustaceans. There are no known ghost crab predators in Cape Verde Islands, unless when they are used as bait by fishermen. Of the seven studied beaches, those two mixed beaches were probably the most used for fishing activities, which could possibly justify the low density values, however it eventually represents insignificant proportions of the population. Also, ghost crabs are generalist and opportunist predators, feeding on several levels of the food chain (Lucrezi and Schlacher, 2014). An alternative food source, easier to obtain may result in ghost crabs neglecting nest predation. In Ribeira Baia (mixed beach), the beach with more fishing activity of all, a large amount of by-catch sharks are drop off on the beach, which can justify the intermediate values of density and the lower nest predation.

Although mixed beaches showed low levels of predation and low ghost crab's density, they revealed a great mortality rate, essentially due to undetermined causes (other causes than predation or inundation) such as temperature, fungal and bacterial infections, root desiccation, etc. In fact, in those beaches the average value of mortality by other causes was almost double the other beaches and hatchery's value. Those causes weren't directly tested in this study, but some mixed sand nests were found completely covered of white and pink fungus, others placed near vegetation had some roots stuck to the shell while others had no evidence of any cause, with perfect white shells with dead embryos. These undetermined causes that affect the embryonic development of sea turtle's eggs may be the same causes that are controlling the distribution and predatory activity of ghost crabs, which could be a possible hypothesis to explain the low predation impact on intermediate sand coloration beaches. There is also the possibility of the ghost crab predating some eggs that otherwise would be dead due to temperature. This last scenario can justify the absence of the impact of temperature on dark sand beaches and the high mortality levels on mixed beaches, since the low predation impact allows eggs to be killed by other causes such as temperature. To proper assess the direct impact of sand temperature on nest survival in all beach types, a similar study should be performed with nest protection, to eliminate the predation impact.

The results also suggest a negative association between the nesting success and the predation rate of the beaches and the beach types: beaches with higher nesting success (and nest density) corresponded to the beaches with lower ghost crab predation rate and, in the opposite, the beaches with higher ghost crab predation registered lower number of nests (lower nesting success and nest density). Marco (2013) suggested that, based on a similar study on different coloration beaches on Maio Island, nesting females do not seem to choose the nesting beach according to sand coloration or through the sand temperature, since they continue to nest on harmful dark beaches when lighter ones are also available. Although the nest site selection is an ambiguous subject, with inter and intra-species variations, maybe the nesting females have the ability to select their nesting site based on ghost crab's density or predation activity, preferring the ones with less activity.

The reason why loggerhead sea turtles continue to nest on such potentially lethal dark sand beaches still needs to be revealed. However, some potential explanations could be: (a) unknown selection criteria; (b) natal homing leads them to those beaches or (c) some plasticity in their philopatry allows them to nest there without selection (Monzón-Argüello et al., 2010; Abella at al. 2010).

This study reinforced the conclusions previously obtained, namely the thermal impact of different sand colorations, showing once again the potentially negative impact of nourishment actions on the reproductive success of sea turtles (Milton et al., 1997; Peterson and Bishop, 2005). Beach

nourishment can easily alter the composition and coloration of the previous sand to a darker one, which may affect the nesting and the hatching success of sea turtles as well as may alter the beach features in such way that it is no longer suitable for nest, forcing females to search for new habitats.

A pioneer investigation has been introduced in the present study by combining the impact of temperature and the predation impact on the reproductive success of loggerhead sea turtles' nests on beaches, allowing a better understanding of the possible interactions between these factors as well as introducing new questions that merit further investigation, such as (a) why warmer sand does not affect the distribution and density of an organism highly reliant on gills' moisture, (b) is the coloration of the mixed beaches that determine their lower predation impact or do they have other features that conditions the ghost crab distribution and density or if (c) there are some selection-based nesting patterns and in which way climate change will affect it.

Regardless of the causes which lead nesting females to nest on dark beaches, it will eventually become an extremely unsafe habitat for nesting, considering the climate changes predictions. Loggerhead sea turtles will have to naturally adjust their spatial (e.g. cooler zones of the beach or new nesting habitats) and temporal (e.g. different nesting season) nesting habits (Hawkes et al., 2007) to cope with the these environmental changes. Despite that, the dark sand beaches may represent a sink habitat in a source-sink system. Thus, and since these beaches still produce viable clutches, it is of great importance to preserve and maintain these nesting habitats as well as the nesting females and the clutch that occur there to maximize the population abundance and to guarantee its heterogeneity.

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Chapter 3

Conclusion and future perspectives

The environmental and biological conditions of nesting beaches are extremely important for successful incubation of turtle eggs. Sand coloration is an important factor in the reproductive success of turtles. Besides the direct impact on sand temperature, sand coloration seems to affect some aspects of the ecology of one of the largest nest predators, the ghost crab *O. cursor*, who does not appear to be affected by thermal conditions.

New lines of investigation should be set out to continue the present study. Further research about the ecology of *O. cursor* (density, size, distribution, nest detection capacity, physiology) and the sand properties of Cape Verde beaches will contribute to better understand the possible interactions between these two factors. A long-term analysis program should be carried out to assess the nesting patterns of loggerhead sea turtle, i.e. assessing the evolution of the nesting activities in dark beaches and whether there is a beach type selection for nesting in the Cape Verde subpopulation. The presence of a beach selection criteria may enhance the reproductive success and the population survival by selecting the more suitable habitats. If sea turtles have no selection criteria, the dark sand beaches will continue to be nesting beaches, though less productive. Future studies, where the variables investigated in the present study are controlled and/or manipulated (e.g. physical exclusion of predators), should bring new insights into the issues discussed in this work.

Management actions must be taken to preserve the clutches and the nesting females that use those less suitable beaches. Environmental assessments should always be considered when implementing beach nourishment programs, as it may alter the sand composition and, consequently, the sea turtle incubation process. In beaches with great density of nests potentially at risk, the nests should be translocated to the hatchery. In the case of beaches with more dispersed nests, an individual protection against crabs should be applied, as well as ensuring that they are not subjected to flood events. Some shade-inducing structures may also be applied to reduce the sand temperature. The beach night patrol programs should be intensified as they have an important role in preventing poaching. In order to ensure continuous male production, light beaches should be prioritized. However, ideally, all nesting habitats, including dark beaches should be protected to ensure greater heterogeneity and productivity of the population.